Egg Capsules of Some Prosobranchs from the Pacific Coast of Panama[1]

BY

CHARLES N. D'ASARO

Institute of Marine and Atmospheric Sciences, University of Miami, Florida 33149[2]

(6 Text figures)

INTRODUCTION

Oothecae of marine prosobranchs, especially those produced by the larger neogastropods, are often conspicuous in the littoral zone. With the exception of the following, previous publications on gastropods contain few references to prosobranch oothecae and development in tropical marine habitats: Amio (1963; in part), Andrews (1935), D'Asaro (1970), Gohar & Eisawy (1967a, 1967b), Knudsen (1950), Kohn (1961a, 1961b), Laursen (1958), Lebour (1945), Natarajan (1958), Ostergaard (1950), Risbec (1921, 1932, 1935), Struhsaker (1966). Thorson (1940), and assorted papers on individual species. Molluscan diversity and abundance in tropical regions have been noted often as Keen (1958) does for the Panamic faunal province, but rarely is information on reproduction included. Therefore, the purpose of this report is to add information on the life histories of certain Panamic species, including several important to aquaculturists and other scientists.

METHODS

The report is based on specimens collected by Dr. F. M. Bayer of the Institute of Marine and Atmospheric Sciences, University of Miami. Adult prosobranchs were transported to the Institute's laboratories in Miami, Florida, where they were maintained in aquaria with circulating sea water for over six years. During this period spawn was obtained from *Anachis fluctuata, Anachis varia, Bursa caelata* (=*corrugata*) (Broderip, 1833), *Jenneria pustulata* (Lightfoot, 1786), *Muricanthus radix* (Gmelin, 1791), and *Vitularia salebrosa*. Egg masses from *Bursa corrugata* and *Jenneria pustulata* were described previously (D'Asaro, 1969a, and 1969b). *Muricanthus radix* produced several egg masses which were distinctly abnormal; therefore, they were not described. The remaining material is examined in this report.

Specimens were preserved in 10% sea-water formalin. Illustrations were prepared by the author from camera lucida drawings of fixed material. Terminology used in the descriptions is the same as that used by D'Asaro (1970). Averages are based on five or more samples. The systematic arrangement follows Keen (1958). A summary of the data is presented in Table 1.

Vitularia salebrosa (King & Broderip, 1832)

(Figures 1a and 1b)

Oothecae from this species were collected from Venado Island in the Bay of Panama on December 24, 1965 attached to the nacreous interior of a pelecypod shell. Mature animals spawned in the laboratory from October through January. Egg masses were deposited on the glass sides of aquaria close to the surface film. In several instances capsules were placed above the surface film and consequently did not develop normally. The spawn forms a flat sheet irregular in outline with the oothecae arranged lineally at 1 mm intervals. Adjacent capsules in a row are usually oriented in the same direction as indicated by the almost continuous apical sutures. A mass may contain from 50 to 400 capsules with an average of 190. Communal spawning does occur in the restricted environment of a 60 liter aquarium where only limited space is avail-

[1] Contribution No. 1175 from the Institute of Marine and Atmospheric Sciences, University of Miami. This investigation was conducted under the auspices of the U. S. Public Health Service (GM 125-41-02), H8179.

[2] Present address: Department of Biology and Marine Sciences, The University of West Florida, Pensacola, Florida 32504.

Table 1

A Summary of Data on the Spawn
of Panamanian Prosobranchs

Species	Average Number Capsules/Mass	Average Number Eggs/Capsule	Average Number Eggs/Mass	Capsular Dimensions H - W - T (mm)	Type of Development[3]
Vitularia salebrosa	190	520	99 000	2.0 - 2.5 - 2.1	pv
Anachis fluctuata	98(2)	24	2 400	1.7 - 0.9 - 0.7	pv
Anachis varia	17[4]	78	–	3.5 - 1.6 - 1.4	pv
Melongena patula	29(1)	–	–	53.0 - 50.0 - 2.0	–
Fasciolaria salmo	106(3)	1 900	201 000[5]	18.0 - 13.0 - 6.0	dd
Conus ximenes mahogani	34	1 100	37 000	7.0 - 7.0 - 1.0	pv

[3] dd - direct development; pv - planktonic veliger
[4] incomplete
[5] includes nurse eggs

able near the surface film. No direct information is available on breeding habits in the natural habitat; however, one egg mass from Venado Island included spawn from another muricid.

The opaque, white capsules are columnar with rounded apices and flared out bases, and are roughly ellipsoid in cross-section (Figures 1a and 1b). Apically, each structure is marked by a central, transparent escape-aperture (Figure 1b). A distinct suture, interrupted only by the escape-aperture, divides the capsule into equal halves in a plane with the long axis of the ellipse and extends into the basal membrane on both sides. During spawning, the basal membranes are fused into a common, transparent sheet which holds the mass together. Variations in color from white to a light pinkish-brown are due to progressive development of the embryo's light brown protoconch and scattered, pigmented granules in the tissues. The average capsular dimensions are: height, 2.0 mm; width (at the base), 2.5 mm; thickness, 2.1 mm. The number of embryos per capsule varies from 380 to 650 with an average of 520. Embryos are nourished by capsular albumen. No nurse eggs are involved. This species, which was reared in the laboratory for two weeks, has a long-term planktotrophic veliger stage.

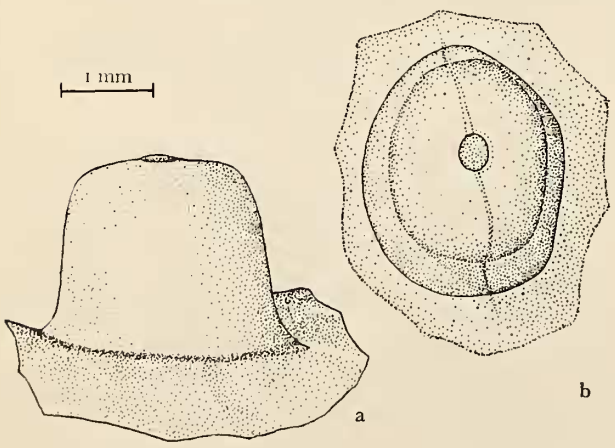

Figure 1

Egg Capsules of *Vitularia salebrosa*
a: lateral view including a portion of the basal membrane
b: apical view

Anachis fluctuata (Sowerby, 1832)

(Figures 2a, 2b, and 2c)

Adult specimens were collected from Venado Island on December 24, 1965 and maintained in aquaria. On March 24, 1967 two egg masses were produced by these animals. The flat, irregular masses, arranged in rows containing 5 to 11 units, were attached to the aquarium glass near the bottom and contained 94 and 101 capsules.

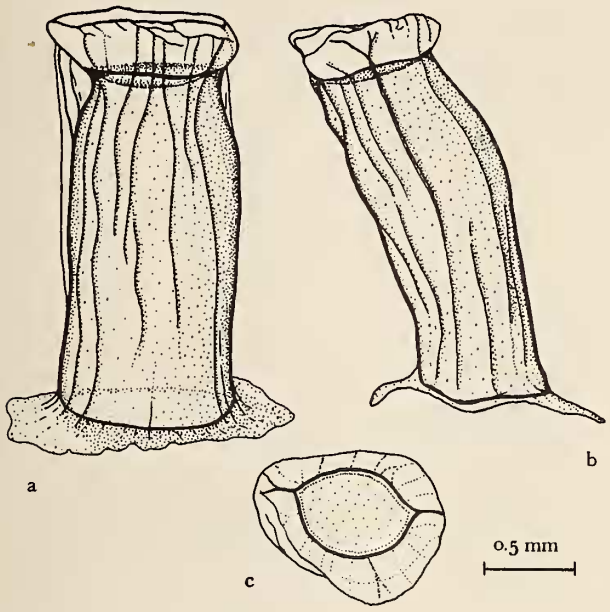

Figure 2

Egg Capsules of *Anachis fluctuata*

a: convex side (tilted toward the viewer)
b: view of the apical plate only
c: lateral view of a tilted capsule

Anachis fluctuata has transparent oothecae which are roughly columnar, marked by multiple, uneven, longitudinal ridges on all sides, and have a wide, collar-like membrane surrounding the apical plate (Figures 2a and 2b). The normally convex sides may be flat or even concave. Most longitudinal ridges extend into the apical membrane and occasionally the basal membrane. On both sides, a single extension of a longitudinal ridge forms a distinct keel bridging the constricted area at the apex (Figure 2a). One keel is usually larger. Laterally, the capsules appear tilted (Figure 2b). The apical plate, which is roughly ovate and slightly wider than the body of the capsule, is outlined by a suture forming the escape-aperture (Figure 2c). There is no peduncle. The oothecae are connected by a continuous basal membrane. Average capsular dimensions are: height, 1.7 mm; width (of the capsule), 0.9 mm; width (of the apical membrane), 1.1 mm; thickness, 0.7 mm. The capsules contained between 17 and 27 embryos, averaging 24. Embryos hatch as advanced veligers which remain in the plankton for only a short period.

Anachis varia (Sowerby, 1832)

(Figures 3a and 3b)

Egg masses and spawning adults were collected from Venado Island on December 24, 1965, under rocks exposed at low tide. The field sample obviously represents a fragmentary egg mass, since only 17 oothecae attached to a shredded basal membrane were included.

The transparent, yellowish oothecae are roughly vasiform, flattened, heavily ribbed and have a raised, apical escape-aperture (Figures 3a and 3b). Three uneven, longitudinal ribs, a large central and two laterals, mark the widest sides. These may appear singular or multiple. In the latter case, the ribs are often constructed of slightly separated, nearly parallel ridges (Figure 3a). A section of the apical plate containing the escape-aperture is elevated and surrounded by a very narrow, transparent membrane raised from the surface. In most cases, the oval exit is covered by an opaque membrane. In addition, the apical plate has sharp ridges extending around the periphery and occasionally from the apertural ridge to the intersection of a lateral ridge. Other randomly placed, low folds may occur. No distinct peduncle is present; however, supporting ribs in the area connect the lateral ribs to the basal membrane. The average capsular dimensions are: height, 3.5 mm; width, 1.6 mm; thickness, 1.4 mm.

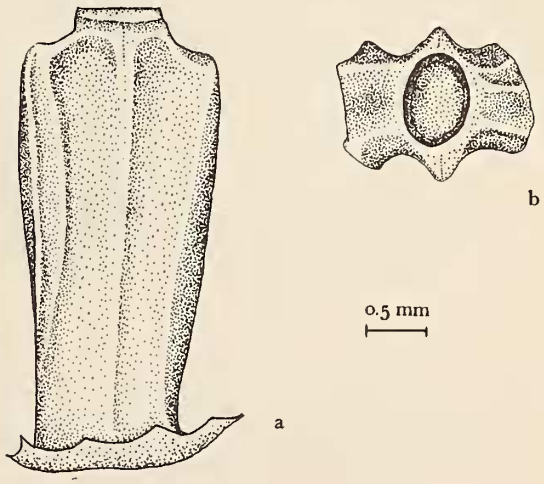

Figure 3

Egg Capsules of *Anachis varia*

a: lateral view including a portion of the basal membrane
b: apical view

Oothecae in the fragmentary mass contained an extremely uniform number of embryos, averaging 78. The enclosed embryos appear to be typical of species with planktotrophic veligers.

Melongena patula (Broderip & Sowerby, 1829)

(Figures 4a and 4b)

Several fragmentary egg masses collected on August 28, 1965 at Venado Island were identified by the collector as *Melongena patula*. Morphologically, the oothecae resemble the egg capsules of *M. corona* (Gmelin, 1791) from South Florida (Clench & Turner, 1956) which are proportionally thicker but do not have serially fused peduncles. The extreme size of the Panamanian oothecae is indicative of a large prosobranch like *M. patula* which may be 10 inches long (Keen, 1958). A total of 29 capsules from a single mass was examined.

Oothecae of this species are flat, opaque, membranous envelopes entirely lacking sculpture (Figure 4a). The edges, where the membranes fuse, are thin and almost knife sharp. There is no apical plate. Instead, the envelope's border corresponding to the apex is unevenly indented (Figures 4a and 4b). A narrow suture in the

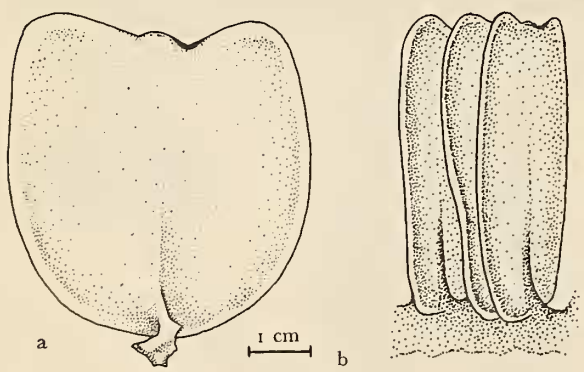

Figure 4

Egg Capsules of *Melongena patula*

a: view of the flat side with the apical suture accentuated
b: three capsules shown in lateral view

fused membrane at the base of the deepest indentation forms the escape-aperture. Each capsule has a solid peduncle with two supporting ribs on opposite sides placed at right angles to the envelope's plane (Figure 4b). These supports extend only a short distance toward the apex as distinct ridges. Adjacent ribs are fused, connecting the capsules in a chain spaced about 6 mm apart. The oothecae have the following average dimensions: height, 5.3 cm; width, 5.0 cm; thickness (at the base), 0.2 cm. No embryos were present in the material examined.

Fasciolaria salmo (Wood, 1828)

(Figures 5a, 5b, 5c, and 5d)

Three large egg masses of this common species were collected from barnacle covered rocks on mud and sand flats around Venado Island on December 24, 1965. There was no direct evidence indicating the number of individuals involved during spawning. The masses are layered and compartmented with the largest containing 4 layers. Each capsule is oriented facing in the same direction as others in a given layer. However, adjacent groups are often situated at various angles or face the opposite direction. Two possible explanations can be given to account for this variation. *Fasciolaria salmo* could be an intermittent spawner pausing frequently, or more likely, it is a communal spawner. Behavioral patterns of this type were noted in the genus by Gohar & Eisawy (1967). According to Keen (1958), the animals are 4 to 5 inches long. At this size they should be able to produce egg masses containing a maximum of 150 capsules. Since the larger clusters examined contained approximately 225 oothecae, considerably more than expected from a 5-inch specimen, communal spawning probably occurs. The masses contained 24, 70, and 225 capsules. Clusters within each contained from 18 to 54, averaging 40.

Fasciolaria salmo has vasiform capsules which are characteristic and typical of the genus. The opaque oothecae have flattened or slightly convex sides, one side having a few low ridges or none and the other is divided into two sections by a sharp keel (Figures 5a, 5b, and 5c). Often low ridges appear on either side of the keel (Figure 5c). Sharp ribs line the lateral edges of the capsules and are continuous with the peduncle (Figure 5b). The apical plate is surrounded by a thickened rib with a sharp edge which flares over the concave side as a large membranous lappet giving the apical region the shape of a conventionalized heart with a raised area where indented (Figure 5d). An oval escape-aperture, covered by an opaque membrane, is situated close to the border of the keeled side. Sutures extend from opposite sides of the oval to the membranous flap (Figure 5d). The peduncle is solid, and typically has supportive ribs. As expected, the basal membranes are fused. Average capsular dimensions are:

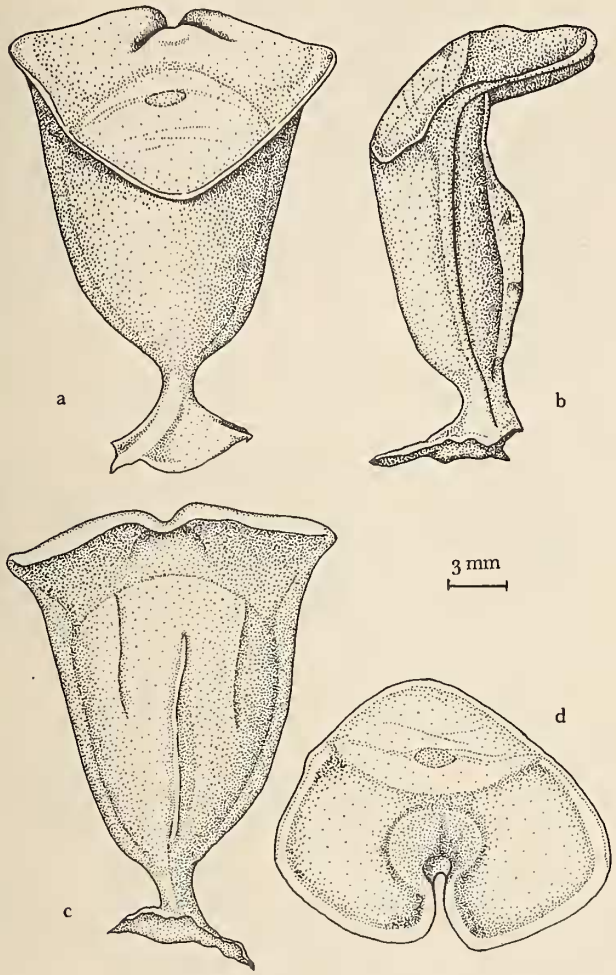

Figure 5

Egg Capsules of *Fasciolaria salmo*

a: view of the smooth, convex side
b: view of the ribbed side showing the keel in lateral view
c: view of the keeled side
d: apical view

height, 1.8 cm; width (capsule), 1.3 cm; width (membranous flap), 1.5 cm; thickness, 0.6 cm. The number of embryos per capsule ranges from 1800 to 2100, averaging 1900. Since the spawn was collected shortly after oviposition, it was not possible to estimate the number of viable embryos. Nurse eggs are common in this genus; therefore, most eggs are expected to be of that type. Direct development is most probable.

Conus ximenes mahogani Reeve, 1843

(Figures 6a, 6b, and 6c)

Two egg masses were collected from sand flats around Venado Island on December 24, 1965. Both were attached to the sand surface of polychaete tubes. In the collector's opinion, *Conus ximenes mahogani* is most probably the spawner since it is especially common in the area. Capsules are generally arranged lineally about 1 mm apart. All spawn present on a given polychaete tube, even if several small masses were included, was considered the production of a single female. The author has observed spawning cones, which normally produce discrete egg masses, depositing isolated egg clusters near a large central mass. The spawn contained 29 and 39 capsules.

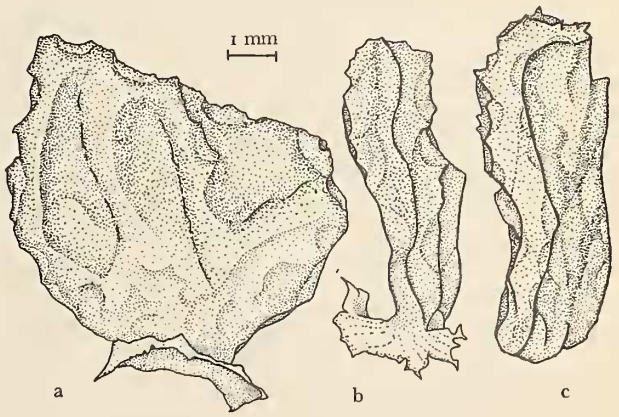

Figure 6

Egg Capsules of *Conus ximenes mahogani*

a: view of the flattened, ridged side
b: lateral view
c: apical view of the sigmoid plate and part of one side

Conus ximenes mahogani has flattened, vasiform capsules with irregularly corrugated and crenulated surfaces (Figures 6a and 6b). The abbreviated peduncles are positioned somewhat off center with the edge opposite the peduncular region being longer. Sculpturing on the sides is patterned only in that there are usually one or more poorly defined ridges running from the central apical region to the peduncle (Figure 6a). Most capsules have a crenulated apical plate with a roughly sigmoid shape (Figure 6c). No definite escape-aperture was observed. Basal membranes are narrow and often discrete. Average

capsular dimensions are: height, 7.0 mm; width, 7.0 mm; thickness, 1.0 mm. The capsules contain from 970 to 1300 embryos with an average of 1100. This species has a planktotrophic veliger.

DISCUSSION

Prosobranch adaptability is again demonstrated by the spawning habits of *Vitularia salebrosa*. This species easily adjusts to a new environment and even to strange food-organisms, requiring only the proper temperature, a hard substrate, and abundant food to produce large egg masses. Finding the proper food remains a problem in spawning some species in the laboratory. For example, specialized carnivores like certain cypraeaceans accept a limited number of colonial ascidians as food and require the food organisms in which to deposit egg capsules.

Columbellids present an interesting example of the caenogenetic variations which often appear in the Prosobranchia. *Anachis fluctuata,* for example, has roughly columnar, ridged oothecae with a wide, collar-like apical membrane. This type is not common to the family or even to the genus. As Thorson (1940) noted, 5 or more different types are found in *Columbella* alone, ranging from stalked structures to semi-globular oothecae with one or more collar-like membranes around the apical region. *Anachis* has a similar range in structural types. Egg capsules of *A. avara* described by Scheltema (1963) are conical and unribbed. *Anachis varia* has roughly vasiform, flattened and heavily ribbed oothecae without distinct peduncles. The columnar structure of the oothecae of *A. fluctuata* also differs and most resembles that of members of the genus *Columbella* with a similar collar-like membrane. In general, these variations indicate that the columbellids are in a state of evolutionary flux, especially when compared to more stable, large groups like the conids or strombids, each having many species with very similar oothecae.

Many similarities exist between the oothecae of *Melongena patula* from Panama and *M. corona* from South Florida and the Gulf of Mexico. Spawn from *M. corona* examined by the author and others (Clench & Turner, 1956) has proportionately thicker capsules and unfused peduncles attached to flat basal membranes. In *M. patula,* ribs on either side of the peduncles fuse to each other as well as to the basal membrane. The resulting structure is somewhat similar to the central rib of xancid spawn (D'Asaro, 1970) and probably is formed in a similar manner.

Oothecae deposited by *Fasciolaria salmo* differ significantly from other fasciolarids in having a large, indented lappet extending from the apical plate. By comparing spawn from the fasciolarids of Florida and the Caribbean, it is possible to establish that the lappet is homologous with the expanded apical rib or ridge found in these species.

Of the 5 species examined in this report, *Conus ximenes mahogani* produced comparatively the least variable spawn. The oothecae are typically conid in their linear arrangement and general shape. The best references for comparative data on the Conidae are by Kohn (1961a and 1961b).

ACKNOWLEDGMENTS

The egg masses examined herein were collected in Panama or obtained from laboratory reared specimens from the same location by Dr. F. M. Bayer of the Institute of Marine and Atmospheric Sciences, University of Miami. The author is greatly indebted to Dr. Bayer for allowing him to study and report on the collections.

LITERATURE CITED

Amio, M.
1963. A comparative embryology of marine gastropods, with ecological considerations. Journ. Shimonoseki Univ. of Fisheries 12 (2, 3): 229 - 358

Andrews, E. A.
1935. The egg capsules of certain Neritidae. Journ. Morph. 57: 31 - 59

Clench, William James & Ruth Dixon Turner
1956. The family Melongenidae in the Western Atlantic. Johnsonia 3 (35): 161 - 188;

D'Asaro, Charles N.
1969a. The egg capsules of *Jenneria pustulata* (Lightfoot, 1786) (Gastropoda: Cypraeacea) with notes on spawning in the laboratory. The Veliger 11 (3): 182 - 184; 1 text fig.; 1 table (1 January 1969)

1969b. The comparative embryogenesis and early organogenesis of *Bursa corrugata* Perry and *Distorsio clathrata* Lamarck (Gastropoda, Prosobranchia). Malacologia (in press)

1970. Egg capsules of prosobranchs from South Florida and the Bahamas with notes on spawning in the laboratory. Bull. Mar. Sci. (in press)

Gohar, H. A. F. & A. M. Eisawy
1967a. The egg-masses and development of four taenioglossan prosobranchs from the Red Sea. Pub. Mar. Biol. Sta. Ghardaqa 14: 109 - 147

1967b. The egg-masses and development of five rachiglossan prosobranchs from the Red Sea. Pub. Mar. Biol. Sta. Ghardaqa 14: 215 - 268

KEEN, A. MYRA
1958. Sea shells of tropical West America; marine mollusks from Lower California to Colombia. i - xi + 624 pp.; 10 colored plts.; 1700 text figs. Stanford Univ. Press, Stanford. Calif. (5 December 1958)

KNUDSEN, JØRGEN
1950. Egg capsules and development of some marine prosobranchs from tropical West Africa. Atlantide Rep. 1: 85 - 130

KOHN, ALAN JACOBS
1961a. Studies on spawning behavior, egg masses, and larval development in the gastropod genus *Conus*. I. Observations on nine species in Hawaii. Pacif. Sci. 15: 163 - 180
1961b. Studies on spawning behavior, egg masses, and larval development in the gasteropod genus *Conus*. II. Observations in the Indian Ocean during the Yale Seychelles expedition. Bull. Bingham Ocean. Coll., Peabody Mus. Nat. Hist., Yale Univ., 17 (4): 3 - 51; 10 tables; 26 text figs.

LAURSEN, D.
1953. The genus *Janthina*. Dana Report 38: 1 - 40

LEBOUR, MARIE V.
1945. The eggs and larvae of some prosobranchs from Bermuda. Proc. Zool. Soc. London 114: 462 - 489.

NATARAJAN, A. V.
1958. Studies on the egg masses and larval development of some prosobranchs from the Gulf of Mannar and the Palk Bay. Proc. Indian Acad. Sci. B. 46: 170 - 228

OSTERGAARD, JENS MATHIAS
1950. Spawning and development of some Hawaiian marine gastropods. Pac. Sci. 4 (2): 75 - 115.

RISBEC, JEAN
1921. Note sur la reproduction de quelques prosobranches néo-calédoniens. Ann. Inst. Oceanogr. Monaco 10: 23 - 33
1932. Note sur la ponte et le développement des mollusques gastéropodes de Nouvelle-Calédonie. Bull. Soc. Zool. France 57 (4): 359 - 375
1935. Biologie et ponte des mollusques gastéropodes néo-calédoniens. Bull. Soc. Zool. France 60 (5): 387 - 417

SCHELTEMA, RUDOLF S. & A. H. SCHELTEMA
1963. Pelagic larvae of New England intertidal gastropods. II. *Anachis avara*. Hydrobiol. 22 (1-2): 85 - 91

STRUHSAKER, JEANNETTE WHIPPLE
1966. Breeding, spawning, spawning periodicity and early development in the Hawaiian *Littorina*: *L. pintado* (WOOD), *L. picta* PHILIPPI and *L. scabra* (LINNÉ). Proc. malacol. Soc. London 37 (3): 137 - 166

THORSON, GUNNAR
1940. Studies on the egg masses and larval development of gastropoda from the Iranian Gulf. Danish sci. Invest. in Iran. Copenhagen, Prt. II: 159 - 238